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Australian songbird body size tracks climate variation: 82 species over 50 years

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JLG conceived the study and with LJ designed the specimen sampling; RL, JS, JoS, KI, JLG collected the data and MRES, JLG, TA, AP designed the analysis; MRES, TA, JLG conducted the analysis; JLG wrote the manuscript and all authors contributed manuscript feedback and read and approved the final manuscript.

Title: Australian songbird body size tracks climate variation: 82 species over 50 years

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Abstract

Observed variation in the body size responses of endotherms to climate change may be explained by two hypotheses: size increases with climate variability (*The starvation resistance hypothesis*); size shrinks as mean temperatures rise (*The heat exchange hypothesis)*. Across 82 Australian passerine species over 50 years, shrinking was associated with annual mean temperature rise exceeding 0.012^{o}C driven by rising winter temperatures for arid and temperate zone species. We propose *the warming winters hypothesis* to explain this response. However, where average summer temperatures exceeded 34^{o}C, species experiencing annual rise over 0.0116^{o}C tended toward increasing size. Results suggest a broad-scale physiological response to changing climate, with size trends likely reflecting the relative strength of selection pressures across a climatic regime. Critically, a given amount of temperature change will have varying effects on phenotype depending on the season in which it occurs, masking the generality of size patterns associated with temperature change. Rather than phenotypic plasticity, and assuming body size is heritable, results suggest selective loss or gain of particular phenotypes could generate evolutionary change, but may be difficult to detect with current warming rates.

Introduction

Animal body size is predicted to decline in response to climate warming, in line with the global pattern of size variation known as Bergmann's Rule: smaller bodies tend to be associated with warmer, lower latitude climates and larger bodies with cooler higher latitudes [1], although the mechanisms underlying variation in body size remain contentious [2]. This relationship between body size and climate has also been observed across geological timeframes with reductions in body size associated with warming climates over millenia [3,4]. The nature and scale of these patterns have given rise to the prediction of pervasive

reduction in body size as the climate warms [4,5]. Because body size directly affects energy and water requirements for thermoregulation, and rates of energy uptake and expenditure [6,7,8], changes in body size have implications for thermal biology and energetics with consequences for individual fitness and thus population dynamics.

Despite the prediction of declining body size, studies have reported considerable variation in climate-related size trends over the last 50-100 years. While some species have declined in size, others have increased or shown no change over time [reviews: 9-12]. Two hypotheses have been advanced to explain this variation in endotherms. The heat exchange hypothesis [sensu 13] suggests that smaller body sizes will be favoured in a gradually warming climate because smaller bodies are more efficient at dissipating heat; this explanation relates to a mechanistic link with thermoregulation, either in relation to increased capacity for heat dissipation [14] or a reduction in the need for heat conservation [15].

The starvation resistance hypothesis (also known as the fasting endurance hypothesis) suggests that unpredictable environments should favour larger-bodied individuals because larger size increases resistance to starvation via capacity to carry more body reserves [8,16]. Energy stores increase with body size faster than does metabolic rate, so resistance to starvation will increase with increasing body size [17]. In the context of climate change, [18] suggested that observed increases in climate variability may reduce the predictability of resources, with potential to increase starvation risk, hence selecting for increasing body size with improved capacity to endure extreme events.

A special case of the starvation resistance hypothesis relates to the increase in frequency of heatwaves that is associated with a warming climate [19]; more frequent and extreme heatwaves are an important signature of current climatic variability [20]. Smaller individuals

exposed to heatwaves use disproportionately more energy and water to dissipate heat than larger individuals (due to their greater surface area to volume ratio), while having proportionately fewer reserves available [21,22]. Larger-bodied individuals are expected to be favoured in such events, particularly when environmental temperatures exceed body temperature and the only avenue for dissipating heat is via evaporative cooling [22, 23]. This hypothesis implies climate-related hard selection via size-dependent mortality; smaller individuals will be selected against in heatwaves leading to a mean increase in the body size of populations over time. When ambient temperatures regularly exceed body temperature, smaller body size ceases to be an advantage but becomes a liability.

Here, we test these hypotheses using a large dataset of body size measurements of 82 species of Australian birds from the Infraorder Meliphagides [*sensu* 24], formerly Meliphagoidea, a large and diverse radiation of Australasian passerines that include the honeyeaters, fairy-wrens, pardalotes, thornbills and allies [25] (Table S1). We characterised changes in body size for each species over the last ca 50 years (1958-2010), during a period of rapid climate change, using 12,029 museum specimens sampled from multiple populations across the distribution of each species (Fig. S1). We then calculated the change in annual mean temperature, annual mean monthly rainfall and annual mean maximum summer temperature in each species' distribution over the same 50-year period. We predicted that (1) body size will tend to decrease over time more in species that have experienced larger increases in mean ambient temperature over time (the heat exchange hypothesis); (2) body size will tend to increase over time in environments with higher summer maximum temperatures that regularly exceed body temperature (the starvation risk hypothesis).

Methods

116 *Study Species*

117 Our study focused on species from the Infraorder Meliphagides [*sensu* 24], formerly
118 superfamily Meliphagoidea), the largest radiation of Australasian passerines, consisting of
119 five families and some 276 species of which 145 are Australian; they comprise almost one
120 third of Australia's passerines [25]. The group comprising honeyeaters, fairy-wrens,
121 pardalotes, thornbills and allies, displays great diversity in life history, ecology and
122 morphology, spanning a wide range of body sizes (6-260 g) and climatic regions (from desert
123 to tropics), and together with their well-resolved phylogeny [25,26], they are an ideal group
124 for investigating responses to environmental change.
125
126 *Museum specimens*
127 Specimens examined from the major museums in Australia were collected between 1960 and
128 2010 (Table S1). Specimen localities spanned about 35^{o} of latitude (10 to 45^{o} S). We sampled
129 multiple populations across each species' range in Australia, including Tasmania (Fig. S1) in
130 order to minimise effects of local factors that can affect body size, such as predation pressure
131 and intraspecific competition. We aimed to quantify species-level responses to broad
132 environmental change, testing overaching hypotheses for causes. For each species, we
133 examined between 20 and 702 specimens (mean 146) (Table S1). We included 11 species
134 with <50 individuals because, although sample sizes are small, these species are relatively
135 well sampled for their small ranges (Table S1). Eight of the 11 species with the smallest
136 sample sizes also have some of the smallest ranges, and so are relatively well-sampled (Table
137 S1). The remaining 3 species (pied honeyeater, *Certhionyx variegatus*, black honeyeater
138 *Sugomel niger*, striped honeyeater, *Plectorhyncha lanceolata*) occur in relatively large
139 ranges. However, these species are nomadic and/or irruptive following good conditions so
140 their core range/distribution is smaller than the range maps would indicate (Fig. S1). All

occur in the more extreme (and remote) arid environments which are difficult to sample but represent important species in the context of the questions we address.

Body size measurement

We measured the length of the flattened wing chord from the carpal joint to the tip of the longest primary, recording to 0.5mm using a butt-ended ruler, as a measure of structural body size. Each species was measured by a single observer. Among passerines, wing length is the best linear predictor of body mass, and accordingly may be used as an index of body size [27]. Some authors have used tarsus or culmen length as indices of body size because these traits are less variable across an individual's life. However, both are subject to Allen's Rule, which predicts a decrease in such traits with increasing latitude, opposite to Bergmann's Rule [28]. This is because in warmer climates appendages of endotherms that play a role in thermoregulation as a source of heat loss will be larger to allow for dissipation of heat loads [29]. Thus, as temperatures rise, increases in bill and tarsus length are predicted and have been demonstrated in several bird species [29, 30]. From the associated metadata we recorded the sex, year of collection and location (latitude, longitude) at which each specimen was collected. We estimated two additional parameters using Geographic Information Systems: altitude, estimated from the latitude and longitude from each specimen, and nearest direct line (orthodromic) distance to the coastline. We used distance to coast instead of longitude as a measure of geographic location because individuals at the same longitude may experience very different temperatures depending on their position relative to the coast. We assigned an abrasion score of 1-12 based on month of capture, with 1 = new feathers assigned to birds captured in March and 12 = old, abraded feathers for captures in February. This is based on our knowledge of moult in Australian birds - most species moult Dec-March after breeding.

166 *Data sets*

167 *(a) Body size*

168 We measured 12,667 individuals of 93 species from the Infraorder Meliphagides [*sensu* 24],
169 formerly superfamily Meliphagoidea) (Table S1). We excluded known juveniles and
170 immatures based on skull ossification recorded during specimen preparation and available
171 from the associated metadata, individuals for which there was no month of capture because
172 abrasion score could not be estimated and 545 individuals for which no sex was recorded
173 from gonads and the sexes were not dichromatic.

174

175 *(b) Climate data*

176 We extracted climate data for the distribution of each species. These data were generated
177 using the ANUClimate 1.0 spatial model [31]. This model produces monthly Australian
178 climate variables for the period January 1970 to December 2013 on a 0.01° longitude/latitude
179 grid interpolated from Australian Bureau of Meteorology national point climate data. We
180 collated monthly estimates of rain, minimum temperature and maximum temperature for the
181 years 1970 to 2012 (one raster for each month x year x climate variable combination). We
182 then extracted summary values for each raster from within each species range (we converted
183 the species range to a raster and used this as a mask for zonal statistics on the climate rasters).
184 These summary values were then tabulated to a .csv file for each species.

185

186 *(c) Climate variables*

187 We created climate variables as follows. Change in annual mean temperature: we calculated
188 the mean temperature for each year for each species, based on mean temperature for each
189 month, extracted for all cells in the distribution of each species. We then fitted annual mean
190 temperature as a response variable and year as an explanatory variable fitting models for each

191 species separately to extract the rate of change over time (year estimate), for use in
192 subsequent models. Models were fitted using the "lm" function in R. Mean monthly rainfall
193 was calculated by averaging mean rainfall for each month. Mean summer maximum
194 temperature was calculated by averaging mean maximum temperature for the hotter months
195 in each year, December, January, February. For our post-hoc analysis we calculated the
196 change in mean minimum winter temperature and change in mean maximum summer
197 temperature using the same procedure as described above for estimating change in mean
198 temperature. We defined winter as the months June, July, August and summer as December,
199 January, February.
200
201 (d) *Climate zones*
202 We calculated the proportion of each species' distribution that occurs in equatorial, arid or
203 temperate climate zones using the Köppen-Geiger climate classification (K-G GIS layer,
204 [32]). We classified species as arid/temperate if >70% of their distribution fell within arid or
205 temperate or arid and temperate zones; tropical species were those with >70% of their
206 distribution in the equatorial zone. Species that were widespread, occurring in both tropical
207 and arid/temperate zones were excluded from our post-hoc analysis.
208
209 *Statistical Analyses*
210 The analysis of the data was done in several steps. First, we estimated temporal change in
211 body size for each species. Then we used these species-specific rates of size change to test for
212 associations between changing climate and body size.
213
214 *(a) Patterns of year-to-year variation*
215 We used generalized additive models to describe patterns of year-to-year variation in body

size, using separate models for each species. The response variable was the wing length of each specimen and the explanatory variables were the year of collection (with a smooth function), latitude, altitude, distance to the coastline, abrasion score and sex of each specimen. All the explanatory variables but the year of collection were centred before the analysis. The models were fitted using the 'mgcv' package [33] in R version 2.15.2 [34]. We assumed a normal distribution and identity link function and estimated the degree of smoothness of the year function using the Generalized Cross Validation with $\gamma = 1.4$ to avoid overfitting [33]. To avoid multicollinearity among the explanatory variables, we first estimated pair-wise Pearson's correlation coefficients between the explanatory variables (Table S2) and confirmed that correlations were not high for any of the combinations ($|r|<0.65$).

To account for model selection uncertainty, we adopted a multi-model inference approach based on AIC (Akaike Information Criterion) [35]. For each species, we first generated a candidate set of models with all possible parameter subsets, which were then fitted to the data and ranked by ΔAIC values (the difference between each model's AIC and AIC_{min}, the value of the "best" model). Models with $\Delta AIC < 2$ are usually considered to have substantial support [35]. We considered species to show important inter-annual variation in body size if they have a smoothed year term in, at least, one of the models with $\Delta AIC < 2$ (Fig S2). For the visual inspection of the estimated smoothed function, we used the result based on the model with the smallest AIC that included the smoothed year term.

(b) Rates of temporal size change

For species showing linear or near linear change in body size across time (effective degrees of freedom < 3 in the full model; edf shows the flexibility of the smoothed function) we

241 calculated the annual rate of size change. After removing 11 species with edf >3, the final
242 data set contained 82 species (Table S1). We fitted separate linear regression models for each
243 species with body size (wing length) as the response variable and year as the explanatory
244 variable, while controlling for sex, age, altitude, latitude and distance to coast when identified
245 in the generalized additive models as important. Residual plots and normal probability plots
246 were used to check for deviations from normality among residuals. All models were fitted
247 using the lm function in R.
248
249 (c) *Comparative analysis*
250 We used Phylogenetic Generalised Least Squares (PGLS) to test for associations between
251 climate and changes in body size over the last 50 years for 82 species of Meliphagides. This
252 approach controls for the phylogenetic relatedness between species by applying a
253 phylogenetic variance-covariance matrix to the linear regression [36]. The analysis was
254 implemented through the R package, *caper* [37]. The phylogeny employed was taken from
255 the maximum likelihood tree produced for the Meliphagides [25], with the tree made
256 ultrametric using the chronoPL function in the ape package [38]. To account for model
257 selection uncertainty, we adopted a multi-model inference approach based on AIC (Akaike
258 Information Criterion) as described above.
259
260 We used the slope of the relationship between body size and year for each species (estimated
261 as described above in 'Rates of temporal size change') as the response variable and fitted the
262 climate variables (change in mean temperature, mean monthly rainfall, and mean summer
263 maximum temperature, and 2 two-way interactions - change in mean temperature : mean
264 summer maximum temperature, and change in mean temperature : mean monthly rainfall) as
265 explanatory variables, controlling for phylogenetic relatedness. All variables were *z*-

266 standardised prior to analysis. Because the response variable comprised single point estimates
267 of the relationship between body size and year without acknowledging the error in those
268 estimates, we also conducted a second analysis where the response variable was a random
269 value taken from the normal distribution with mean equal to the observed estimate, and
270 standard deviation equal to the standard error around that estimate. The final model estimates
271 here were the mean of the estimates derived from 1000 simulations.
272
273 (d) *Post-hoc analyses*
274 To test whether the declines in body size we observed (see results) were associated with rates
275 of warming in winter versus summer, we undertook the following post-hoc analysis. We used
276 the slope of the relationship between body size and year as the response variable and fitted
277 climate variables (change in winter temperature, change in summer temperature, mean
278 summer maximum temperature, mean winter minimum temperature) and two interactions
279 (between mean winter temperature and mean change in winter temperature; and between
280 mean summer temp and mean change in summer) as explanatory variables. We included only
281 arid and temperate species, and controlled for phylogenetic relatedness as in the main
282 analysis. As above, we also repeated the analyses using repeat simulations of the response
283 variable. There were only 8 tropical species in our dataset, too few to detect an effect.
284
285 **Results and Discussion**
286 Annual mean temperature has increased over the last 50 years in 81 of the 82 species'
287 distributions we considered (Fig. 1). In contrast, patterns of mean rainfall showed
288 considerable variation across distributions with some showing increases in mean rainfall and
289 others declines or no change (Fig. 1).
290

Change in mean temperature, rather than summer temperature or rainfall, showed the strongest association with estimates of body size changes across species, and was the only climate variable included in all top models (Table 1). Similar estimates to those in Table 1 were derived from 1000 model simulations where errors in the estimates of body size change were taken into account, providing strong support for this result (Table S3). Declines in body size start to be observed in cases where the rate of mean temperature change within a species' distribution exceeded 0.012^{o}C per year (1.2^{o}C per 100 years), consistent with the heat exchange hypothesis (Fig. 2). Given the diversity of species and habitats included in our analyses, the identification of a rate of temperature change beyond which declines in body size were observed suggests a broad-scale physiological response to changing climate.

Although there was no association between body size and mean maximum temperature *per se*, a shift in the extent and direction of size change was observed for species experiencing both high levels of warming and high summer temperatures (Table 1). Fig. 2b indicates that above about 34^{o}C, no decreases in body size are predicted, regardless of amount of temperature change experienced (all of the model predictions > 0), and for species experiencing greater than 0.0116^{o}C (the point at which the regression lines intersect in Fig 2c), body size may even increase in warmer climates (interaction Tmax x Tmean; Fig. 2; Table 1, Table S3). Increasing body size to increase body reserves as climate variability increases is consistent with the starvation resistance hypothesis in the context of heatwaves. Our result is unlikely to be an artefact of sampling because the species included in the analysis covered the entire range of these two variables: 67% of species (55/82 species) experienced >0.01166^{o}C per year change, with 38 species experiencing mean maximum summer temperatures below 34^{o}C and 17 species exceeding 34^{o}C (Fig. 2). When environmental temperatures exceed body temperature (ca. 40^{o}C) the only avenue for birds to

316 dissipate body heat is via evaporative cooling, with small bodied individuals particularly
317 vulnerable to dehydration and mortality because of their disproportionately large surface
318 areas [21,22]. Smaller individuals thus face twin costs under heatwave conditions: lower
319 energy and water reserves, and disproportionately high rates of water loss. Accordingly, the
320 benefit of smaller body size is plausibly outweighed by the costs of exposure to extreme
321 temperatures during heatwaves.
322
323 Recent work by [39] examined evaporative cooling capacity and heat tolerance in 5 passerine
324 species in Australia's arid zone, including two of the species in this study (yellow-plumed
325 and spiny-cheeked honeyeaters). They confirmed the reliance of these species on evaporative
326 heat loss via panting at high air temperatures, consistent with studies of other Australian
327 passerines. When air temperatures exceeded 38^{o}C rates of evaporative water loss (EWL)
328 increased rapidly and linearly to 7-fold (670-860%) above basal rates [39]. Moreover, rates of
329 EWL scaled negatively with body mass with smaller-bodied individuals more vulnerable to
330 dehydration, consistent with our result. This work accords with recent studies showing that a
331 body temperature of 45^{o}C is the upper limit to physiological function in most birds [39]. In
332 contrast, increase in metabolic rate associated with the onset of panting varied considerably
333 among species, suggesting that dehydration rather than energy balance represents the greatest
334 threat to species in heatwaves [23]. Thus, although our results are consistent with the
335 starvation risk hypothesis, they also suggest the significance of maximizing resistance to
336 dehydration in the face of increasing heatwaves.
337
338 Empirical studies of wild populations identify air temperatures in the mid-30s as potentially
339 harmful, with individuals unable to maintain body condition following prolonged exposure to
340 such temperatures, sometimes leading to size-dependent mortality [40,41]. In a population of

Australian white-plumed honeyeaters, *Ptilotula penicillata*, repeated exposure to daily maxima >35^{o}C in a semi-arid region was associated with increases in mean body size over a time scale of decades, apparently via the loss of small individuals from the population [42]. This effect appeared to be mediated by size-dependent effects of weather on body condition; smaller individuals lost more mass when exposed to high temperatures and were less likely to survive to the following spring [41]. Our observed mean summer temperature threshold of about 34^{o}C, at which no decrease in body size is predicted, is remarkably consistent with empirical studies that identify prolonged exposure to air temperatures >35^{o}C as harmful, and is also consistent with hard selection because the observed change in avian body size aligns with known physiological tolerances associated with fitness [21,22, 23].

Although recent attention has mainly focused on spring and summer temperatures in mediating size changes under global warming, declining body size may also be associated with reduced selection pressures on small individuals experiencing warmer autumns and winters, leading to their higher survival. Winter is considered a challenging time, and can cause direct mortality via cold stress, reductions in immune function, or energetic constraints as a result of resource shortages [43,44]. Indeed, energetic costs of thermoregulation in winter during periods of low food availability can exceed those during the breeding season [43]. Moreover, winter mortality is often observed to be size-dependent with the smallest individuals suffering higher mortality, contributing in part to the widely accepted rule for positive viability selection on body size [45]. Accordingly, reduced selection pressures associated with warming winters may increase the survival of smaller individuals leading to an incremental decrease in mean body size over time; hence we propose “the warming winters hypothesis”. Because animals are acclimatized to local conditions and winter represents the harshest conditions in temperate environments, a release from selection

366 pressures associated with a given level of temperature rise (here 1.2^{o}C/100 years) is likely to
367 have similar effects across all populations, in this case favouring smaller individuals,
368 regardless of the severity of winter conditions experienced.
369
370 By comparison, the decrease in body size we observed across species is less likely to relate to
371 warming summers because the same rate of warming will have different effects on body size
372 depending on the thermal tolerances of individual species and the summer conditions each
373 experiences [7,21]. Only if rising temperatures push individuals beyond the upper bound of
374 the thermoneutral zone (TNZ) - the range of air temperatures where no additional energy and
375 water are specifically allocated to maintain homeostasis - will the adaptive significance of
376 body size change. Because the location of the TNZ varies among species due to differences
377 in body size and shape [7, 23] and phylogeny [46], a given degree of temperature change is
378 likely to affect species differently. Indeed, our post-hoc analysis found that declining body
379 size was associated with increasing winter, but not summer, temperatures for arid and
380 temperate species in line with our warming winters hypothesis (Table 2, Table S4).
381
382 Analysis of long-term data sets of wild populations provide some of the strongest evidence
383 that temporal declines in body size may be associated with a release from winter stress. In
384 Soay sheep, *Ovis aries*, warmer winters have led to higher survival of smaller individuals,
385 leading, in part, to a decline in body size over the last 30 years [47]. A similar pattern was
386 observed in a much milder climate in Western Australia where winters do not generally
387 involve sub-zero temperatures. Warmer winter conditions were associated with higher
388 survival of smaller individuals in two small passerine species monitored over 39 years [48].
389 Although most evidence suggests that shifts in body size are climate related, density-
390 dependent effects (e.g. competition for food) are also likely to be important and drive

391 complex size patterns. However, such effects are likely to be site specific so unlikely to
392 account for the broad scale patterns observed.
393
394 In contrast to species in temperate climates, relaxation in selection pressure is unlikely to
395 account for temporal declines in endotherm body size in the tropics which experience low
396 seasonality and limited temperature range. As temperatures rise, selection pressures in the
397 tropics are more likely associated with increasing costs of keeping cool, favouring smaller
398 body sizes with increased capacity for heat dissipation. James [14] argued that selection for
399 smaller body size is particularly strong in the tropics because high temperatures coincide with
400 high humidity which reduces the gradient driving evaporation, thereby limiting heat loss.
401 Smaller bodies with relatively larger surface areas are therefore advantageous [49]. In
402 addition, the capacity for acclimatization is likely limited for tropical species because they
403 experience narrow daily and seasonal temperature range [50], so a given increase in
404 temperature is likely to impose greater costs on tropical compared with temperate species.
405 Thus, although a warming climate might favour smaller body sizes in both the tropics and
406 temperate regions, the underlying mechanisms may differ. Our dataset included only 8
407 tropical species, and so lacked the necessary power to test for an effect.
408
409 Overall, our study suggests that avian body size is indeed responsive to climate change
410 [contra 12,51], and that climate-driven changes in body size are both temperature-related and
411 founded in a physiological response to changing conditions. Temperature-related effects may
412 account for global patterns of changing body size in the absence of extreme events, (both
413 summer and winter), and regardless of rainfall patterns which have previously been suggested
414 as important in driving selection [52] even though water availability differs between northern
415 and southern hemispheres [53] and rainfall patterns are highly variable at regional scales

[54]. We found no evidence that rainfall directly underlies body size trends at the species level; rainfall and its interaction with mean temperature were included in the top model, but their effects were weak (Table 1). Nevertheless, rainfall can mediate responses to temperature, in both hot and cold conditions, as well as affect foraging behavior and food availability [55,56]. Rainfall is therefore likely to be integrally linked with climate-driven changes in physiology at the level of populations.

More broadly, the suggestion that changes in food availability driven by climate-related changes in primary production underlie observed temporal trends in body size across species [12, 52] seems unlikely on the basis of our results. With the exception of the relatively small alpine zone, primary productivity on the Australian continent is regulated and constrained by rainfall and plant water availability rather than temperature *per se* [54], and climate change impacts on rainfall regimes are varying greatly at regional scales [57]. Accordingly, body size trends we observed across species that inhabit different climatic zones and regions are unlikely to be associated primarily with rainfall-related variation in primary productivity. To further address this issue, we re-ran our main model replacing mean monthly rainfall with change in rainfall (estimated using the same method as for change in mean temperature). Models with rainfall change were a poorer fit to the data compared with the equivalent models using mean rainfall (best model with rainfall change included AIC: 235.0 versus 231.7 for best model with mean rainfall), and the top model did not include rainfall change, (and was the same as model 3 in Table 2), supporting our conclusion. Moreover, in the northern hemisphere, primary production is associated primarily with temperature not rainfall [58], so it seems unlikely that changing primary production underlies global trends in body size if the drivers of productivity differ between hemispheres.

Our findings have important implications. We provide strong evidence for changes in body size as a response to climate change, with multiple mechanisms likely to underlie species' responses. Temporal trends in body size are likely to reflect the relative strength of selection pressures at different times of the year and different phases of a climatic regime, including release from winter conditions as well as increased pressure from summer extremes [e.g. 59]. To date, most studies have focused on the negative consequences of extreme events but our results also highlight the potential importance of relaxation in winter conditions. Given the importance of temperature extremes in this context, birds might indeed be considered the 'canaries in the coalmine' because they are likely to be more responsive to changing climate than are mammals, being diurnal, with small body sizes, and limited in their capacity to store body reserves because of the demands of flight. This may explain, in part, the finding that mammals are less likely to show temporal size change than birds [12].

When analyzing size trends, studies should consider the rate of temperature change experienced, given that our results suggest that declines in body size are triggered only when increasing mean temperature exceeds 0.012^{o}C per year. Studies that include climate variables as predictors often fit static measures, omitting rates of change, and critically ignore the season (window) in which the temperature change has occurred. A recent study by [60] concluded that there was no evidence that warmer mean temperatures are associated with selection for smaller body size. However, our results suggest that a given amount of (mean) temperature change will result in differing effects on phenotype depending on the season in which the temperature change occurs. For example, a given mean temperature change that occurs in winter might be associated with declining size, but not when it occurs in spring. Similarly, selection on body size associated with rising summer temperatures will only be detectable in species where the given increase in mean temperature occurs in summer, and

466 pushes the species beyond its TNZ thereby changing the selection pressure. Attempts to find
467 associations between selection gradients for size and mean temperature change are therefore
468 unlikely to succeed. This is especially the case where selection gradients are derived from
469 differing, often short, timeframes [60], making it even more difficult to detect patterns.
470
471 We agree with [12] that more data are needed on how climatic factors shape selection
472 pressures and the adaptive nature of temporal size trends in relation to climate change.
473 Nevertheless, although most evidence to date suggests that shifts in body size are the result of
474 phenotypic plasticity, our results raise the possibility that change in the composition of a
475 population via the selective appearance or disappearance of particular phenotypes could
476 generate evolutionary change, assuming body size is heritable [61]. However, detecting such
477 shifts may be difficult if rising temperatures are only now reaching levels at which changes in
478 selection pressures may occur, and the translation from effects on individuals to population-
479 level changes in mean body size are likely to be incremental. This may account for difficulty
480 thus far in detecting microevolutionary responses to climate change [62].
481
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660 **Figure Legends**

661

662 **Fig. 1**. Temporal trends in (a) body size (wing length) and (b) mean annual temperature and
663 (c) mean summer maximum temperature and (d) mean monthly rainfall across 50 years (1970
664 – 2010) for 82 species of passerine bird in the Meliphagides. Each line represents a single
665 species, and the order of species is the same in each panel. We calculated mean temperature,
666 mean summer maximum temperature and mean monthly rainfall for each year for each
667 species, based on values for each month, extracted for all cells in the distribution of each
668 species. Solid green dots represent significant change in body size; green circles indicate
669 trends.

670

671 **Fig. 2**. Association between the change in structural body size (wing length) and change in
672 mean annual temperature, given mean maximum summer temperature for 82 species of
673 passerine bird from Meliphagides [*sensu 24*], formerly superfamily Meliphagoidea). (a) 3D-
674 representation of the phylogenetic generalised least squares model predicted relationship; (b)
675 2D-representation showing species data points, PGLS regression lines for the relationship
676 between change in body size and mean summer maximum temperature showing species that
677 experience different degrees of temperature change with PGLS model regression lines for 0,
678 0.004, 0.008, 0.012, 0.013, 0.014. 0.015 and 0.016 ^{o}C increase in mean temperature; (c)
679 similar representation of relationship between change in body size and change in mean
680 annual temperature showing species that experience different mean summer temperatures:
681 model lines represent relationship at 18, 23, 28, 33 and 38 ^{o}C (colours as represented in
682 legend).

683

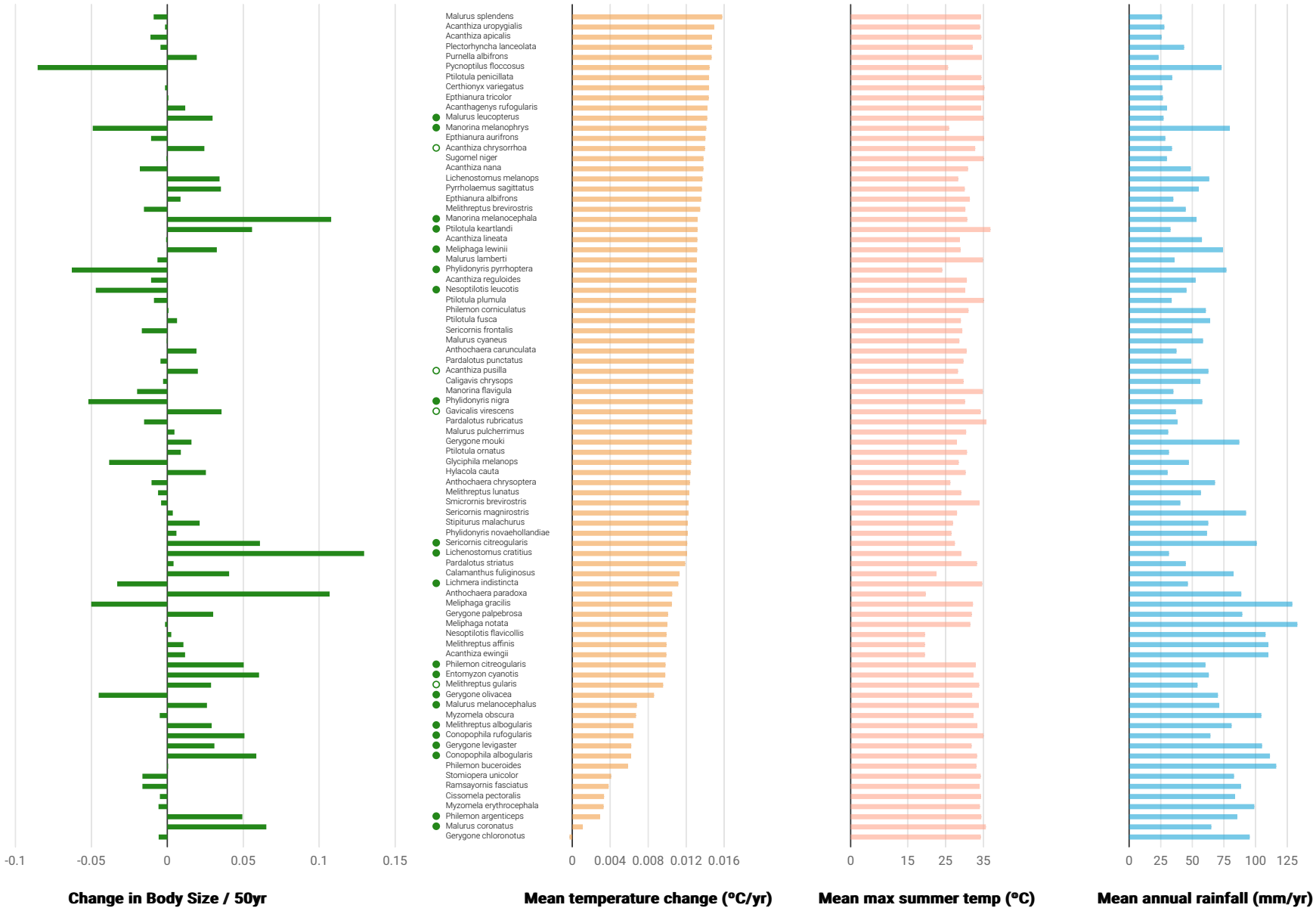
Table 1. Top phylogenetic generalized least squares models (ΔAIC<2) predicting body size changes over time in 82 species of Meliphagides. Predictors are ΔT_{mean}: mean temperature change (°C / year), T_{max}: mean summer maximum temperature (°C), Rain: mean monthly rainfall (mm), and all interaction terms. Response variable is the regression slope estimate of body size over time for the species. All variables were standardised and model estimates (with standard errors) are shown for each model (larger estimates are therefore larger effects). W_i = Akaike weight of the model. Parameter estimates in the models that were statistically significant (at $\alpha = 0.05$) are indicated in bold.

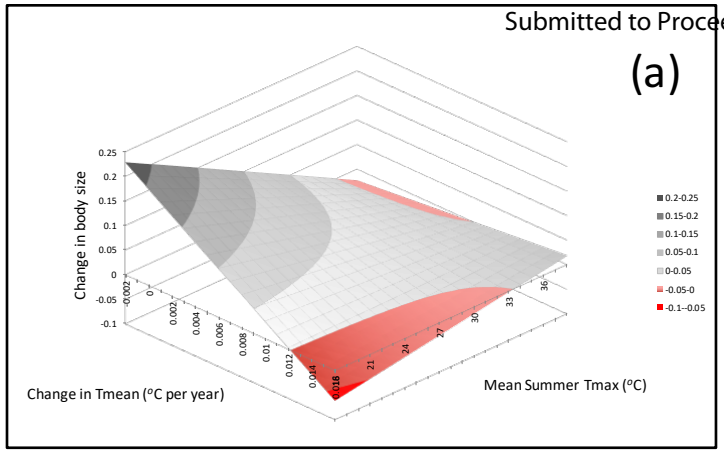
Model	ΔT_{mean}	T_{max}	Rain	ΔT_{mean}:T_{max}	ΔT_{mean}:Rain	R^2	ΔAIC	w_i
1	**-0.904 (0.248)**	-0.133 (0.154)	-0.338 (0.180)	**0.548 (0.211)**	0.317 (0.182)	0.149	0	0.254
3	**-0.682 (0.217)**	-0.229 (0.144)	**-0.361 (0.181)**	**0.403 (0.198)**		0.114	0.879	0.164
4	-0.169 (0.110)					0.029	1.729	0.107

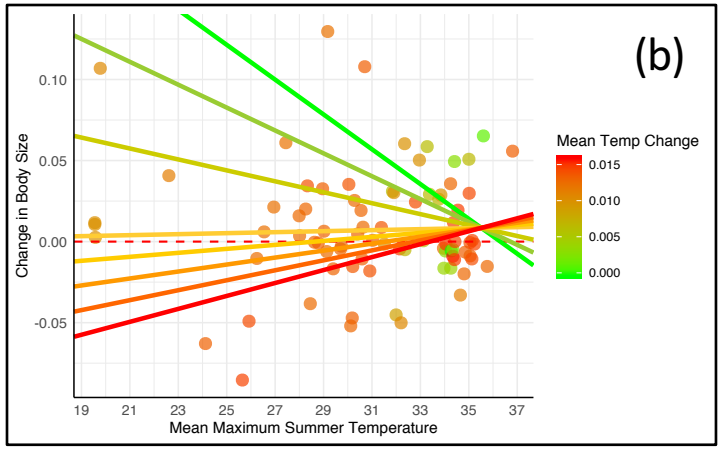
694 **Table 2.** Top phylogenetic generalized least squares models (ΔAIC<2) predicting body size
695 changes over time for 64 temperate and arid zone species of Meliphagides. Predictors are
696 mean minimum winter temperature (T_{winter}), mean summer maximum temperature (T_{summer}),
697 and the mean change over time (°C / year) for both measures (ΔT_{winter} and ΔT_{summer}, for winter
698 and summer temperatures respectively). Response variable is the regression slope estimate of
699 body size over time for the species. All variables were standardized and model estimates
700 (with standard errors) are shown for each model (larger estimates are therefore larger effects).
701 W_i = Akaike weight of the model. All parameter estimates in the models that were statistically
702 significant (at $\alpha = 0.05$) and are indicated in bold.
703

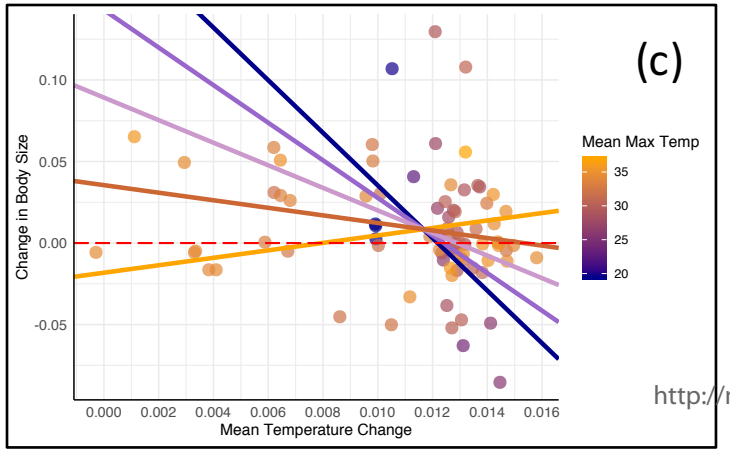
Model	T_{winter}	T_{summer}	ΔT_{winter}	ΔT_{summer}	R^2	ΔAIC	w_i
1	**1.354 (0.535)**	**-1.803 (0.547)**	**-0.978 (0.340)**	0.510 (0.292)	0.349	0	0.187
2	0.837 (0.469)	**-1.294 (0.492)**	**-0.592 (0.277)**		0.257	0.493	0.146
3					0	0.573	0.140
4		-0.540 (0.298)	-0.610 (0.298)		0.136	0.963	0.116
5			-0.178 (0.186)		0.032	1.911	0.072

704


Malurus splendens
Acanthiza uropygialis
Acanthiza apicalis
Plectorhyncha lanceolata
Purnella albifrons
Pycnoptilus floccosus
Ptilotula penicillata
Certhionyx variegatus
Epthianura tricolor
Acanthagenys rufogularis
Malurus leucopterus
Manorina melanophrys
Epthianura aurifrons
Acanthiza chrysorrhoa
Sugomel niger
Acanthiza nana
Lichenostomus melanops
Pyrrholaemus sagittatus
Epthianura albifrons
Melithreptus brevirostris
Manorina melanocephala
Ptilotula keartlandi
Acanthiza lineata
Meliphaga lewinii
Malurus lamberti
Phylidonyris pyrrhoptera
Acanthiza reguloides
Nesoptilotis leucotis
Ptilotula plumula
Philemon corniculatus
Ptilotula fusca
Sericornis frontalis
Malurus cyaneus
Anthochaera carunculata
Pardalotus punctatus
Acanthiza pusilla
Caligavis chrysops
Manorina flavigula
Phylidonyris nigra
Gavicalis virescens
Pardalotus rubricatus
Malurus pulcherrimus
Gerygone mouki
Ptilotula ornatus
Glyciphila melanops
Hylacola cauta
Anthochaera chrysoptera
Melithreptus lunatus
Smicrornis brevirostris
Sericornis magnirostris
Stipiturus malachurus
Phylidonyris novaehollandiae
Sericornis citreogularis
Lichenostomus cratitius
Pardalotus striatus
Calamanthus fuliginosus
Lichmera indistincta
Anthochaera paradoxa
Meliphaga gracilis
Gerygone palpebrosa
Meliphaga notata
Nesoptilotis flavicollis
Melithreptus affinis
Acanthiza ewingii
Philemon citreogularis
Entomyzon cyanotis
Melithreptus gularis
Gerygone olivacea
Malurus melanocephalus
Myzomela obscura
Melithreptus albogularis
Conopophila rufogularis
Gerygone levigaster
Conopophila albogularis
Philemon buceroides
Stomiopera unicolor
Ramsayornis fasciatus
Cissomela pectoralis
Myzomela erythrocephala
Philemon argenticeps
Malurus coronatus
Gerygone chloronotus
-0.1
-0.05
0
0.05
0.1
0.15
Change in Body Size / 50yr
0
0.004
0.008
0.012
0.016
Mean temperature change (°C/yr)
0
15
25
35
Mean max summer temp (°C)
0
25
50
75
100
125
Mean annual rainfall (mm/yr)


(a)
Change in body size
Change in Tmean (°C per year)
Mean Summer Tmax (°C)
0.2-0.25
0.15-0.2
0.1-0.15
0.05-0.1
0-0.05
-0.05-0
-0.1--0.05


(b)
Change in Body Size
Mean Maximum Summer Temperature
Mean Temp Change
0.015
0.010
0.005
0.000


(c)
Change in Body Size
Mean Temperature Change
Mean Max Temp
35
30
25
20